NOTE I.

THE EVOLUTION OF COLOUR IN LEPIDOPTERA

BY

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At the Zoological Congress at Cambridge I imparted, especially for the exclusively English speaking and reading entomological public, some notions on this biological phenomenon, the existence of which I think to have discovered by studying the ontogenesis of caterpillars of Sphingidae, and also in the imagines of several families of Rhopalocera, more particularly in those of the Pieridae; the results of these studies have however been published in German. Now, before the Transactions of that Congress had been published, an article entitled »*The Colours and Pigments of Butterflies*" by Miss M. I. Newbegin appeared in the February number of »Natural Science", in which, besides some other papers of these latter days on the same subject, she also discusses my study on the colour-evolution of Pieridae. Although I have tried at the afore-named Congress to disclose shortly the course of my observations and the results thereof as clearly as possible, from what Miss N. imparts I am afraid one must gather quite a false idea of what I have said. It seems to me she has not read my paper as carefully as might be desirable for anybody writing an article about it, and as a matter of course her judgment necessarily cannot be right. Since it is of the greatest importance for me to be well understood, so that other people may be led to submit my observations to a

new investigation, to amplify them, if they come to see the exactness of the alleged facts and to ponder on my deductions, I think I may not yield to Miss N.'s opinion, but have to express my objections against it. All the more so as it is offering me an opportunity to point out how the different papers published since then on the same subject do not in any way conflict with or refute the justness of my view, as to the main point at least; and further to indicate the way which future investigations will have to follow, to get at results that can bring the necessary light into this matter.

Miss N. is not well disposed towards my theory. No wonder, for she has a theory of her own about animal coloration, and mine does not agree with hers. One of the two must be wrong, partly at least, if not wholly so. This cannot be questioned, but I cannot for all that consider it as a matter of course that mine should be the wrong one, though indeed I am quite willing to admit that this may be the case. To decide this matter, however, a closer examination than Miss N. has devoted to my investigations will be wanted. Nor do I believe this can be done by chemical studies alone; it seems to me, therefore, that Miss N.'s views resting almost exclusively on this basis, bear a too partial character. Certainly a chemical as well as a microscopical inquiry into the nature of colours is a very important thing with reference to the topic of my study, and I too made an ample use of the results obtained thereby, but doubtless it is erroneous to think this the only way in which this matter can be explained. There are people with black or fair or red hair, and surely chemistry and microscopy can reveal very important things as to the nature of these differences in colour, but they certainly never will explain the ethnological and anthropological phenomena of which these differences are the expression. Neither those sciences in themselves will ever be able to explain the biological facts to

which the great difference in colour and wing-pattern among the Lepidoptera is to be attributed.

Since my theory is founded on facts observed by myself, it is absolutely necessary for anybody wanting to judge of it to examine the exactness of the alleged facts. Now this is no light and easy work, requiring a great deal of time besides. As I already pointed out at the beginning of my last paper, one needs to dispose of a sufficiently large material of Pieridae for consultation, as even good pictures can only partially be used for that purpose. And moreover the capacity to make a good use of such material cannot be dispensed with. One has to know how to read fluently the „biological map", as the wing-pattern of Lepidoptera has sometimes been called, a knowledge only to be obtained at the price of a great amount of study. It is a well-known fact that white people on first meeting with coloured men, do not know how to distinguish the one from the other, and that it takes them rather a long time before they are fully up to it. Yet coloured men's features are respectively just as distinct as ours. As everybody is aware a shepherd knows every lamb of his flock though to others all sheep are alike. With butterflies it is exactly the same thing: one must learn to see their respective difference. Pretending to judge of their colour-variations before knowing this, is just as absurd as a white man pretending to study the expression of mental emotions in the face of a negro, before being able to distinguish several negroes' respective features. Now firstly one must have before one's eyes all or at least a great many species of such genera — as for instance *Hebomoia* or *Tachyris* in which the process of colour-change can easily be observed, and then one has to know how to form series by comparison of the occurring colour-phenomena, so as to understand clearly in what manner that change proceeds. This is rather difficult unless one is used to closely observing butterflies. Another thing required for this comparison is to recollect them, all

the more so, if such an investigation is to be extended as to other genera and even to families. So if one is not a lepidopterologist possessed with this capacity such an investigation is not an easy matter.

Now I presume Miss N. is not a lepidopterologist and consequently has not been able to follow my observations in a sufficient manner. Unfortunately this had led her into a very superficial attack on my scientific work, thus obliging me to utter a serious protest.

The authoress seems to consider my theory of colour-evolution in Lepidoptera as resting on a loose hypothesis that has simply arisen in my brain by contemplating over so many butterflies. Now this is quite false. My theory is not founded on mere guessing, but on a fact revealed to me after long observation which, however, had not yet attracted attention. Only so far as it is an hypothesis that the embryological forms revealed by the study of the ontogenesis of an animal do render also those of the phylogenesis of the species, does my theory also rest on an hypothesis. My paper on colour-evolution in Pieridae is not at all a thing by itself; it is founded — as I expressly stated therein — on the results of my former studies of the colour and the polymorphism of caterpillars of the Sphingidae. In that study, based on several ontogenetic observations made by myself as well as by others, I had demonstrated pretty decisively, as I thought, that the primary colour of all these caterpillars is in a state of continual changing, having begun to do so even before the differentiation of the family; and always in a definite direction, but proceeding in every species and also in the individuals in a very irregular way. Now with this change neither the influence of environment nor natural selection has any thing whatever to do, and that is why I concluded to a hitherto unknown phenomenon of evolution called by me »colour-evolution", a phenomenon by which the difference of colour, as well as the polymorphism in those caterpillars, easily can be explained. It has not been

established as yet that my observations and the conclusions derived therefrom are erroneous; that is why I think I may accept the existence of this phenomenon as a scientific fact. This induced me to go on trying to get at an explanation of the difference in colour and the polymorphism of imagines of the Lepidoptera by the same means that proved so satisfactory as to the phenomena of caterpillars of Sphingidae. So that was what led me to write my paper — as I imparted at the late Congress. In no way it is based on a loosely emitted hypothesis.

I regret to state that on the whole Miss N.'s verdict on my work is remarkably superficial, else I think she would not have expressed it in nearly the following terms: the view that »scarlet is the most primitive colour in the »Pieridae with the correlated statement that the males in »the family are frequently more primitive in regard to »their colours than the females, will be found somewhat »difficult of acceptance by most." For in my study »*Ueber die Farbe und den Polymorphismus der Sphingiden Raupen*" [1]) I have already named the fact that in many caterpillars red indeed does not appear as the most primitive colour, but still as one ontogenetically preceding the white colour, the investigations of Dr. Gräfin von Linden — of which I shall speak later on — adding a strong support also in reference to the imagines of many Rhopalocera to this fact, indeed acknowledged and honestly mentioned by Miss N., but of which she does not seem to grasp fully the really great significance. As to the question of sexual preponderance, her words in the first place do not exactly render what I have said, and moreover this opinion of mine is not so very strange or inadmissible. The oldest and most generally adopted view in this matter, Darwin's view, — the only one Miss N. seems to be acquainted with — is that male preponderance always exists. But this opinion did not remain unattacked. Prof. Dr. J. Kennel

1) Tijdschrift voor Entomologie, XL, 1897.

asserted against it that female preponderance always exists among butterflies. And Prof. Dr. Eimer accepted that both, male- and female-preponderance, exist, and founded there on two of his so-called laws. Now against these three opinions I alleged as the results I collected from the facts of colour-evolution observed by me, that indeed both phenomena occur, but that it would be a mistake to derive therefrom any constant rule or law, since they are merely the expression of the enormous difference in susceptibility for evolution — and thus in the course thereof — not only between the familiae and genera but also between the races, sexes and even individuals. This too is often the cause of one sex sometimes presenting itself as more or less primitive than the other. So in fact, in a biological sense every kind of preponderance is excluded. This now appears to me very different from what Miss N. seems to have read in my paper.

Further she says it seems to her a much simpler explanation of the phenomenon which I denominated »colour evolution" to accept that red, yellow and white as chemically nearly related original colours of Pieridae, are readily converted into one another and tend to disappear, as the dark pigments develop, replaced by the brilliant optical colours which are apparently associated both with these dark pigments and with the progressive differentiation of the scales. Now it is my opinion that the strangeness of a new view does not necessarily involve the evidence of its being a false one; that indeed most new things look strange, and that moreover the apparent simplicity of a superficial explanation does not suffice in this matter for its being substituted for the one I gave. Biological phenomena usually are brought about by the coöperation of so many factors that indeed they are anything but simple, in fact rather of a very complex nature, and therefore cannot be explained in such a simple way. Besides that so called simple explanation is not found to be confirmed by what the study of butterflies teaches us. The transition of red

and yellow on butterflies does no more bear an accidental character than that of the colours of Sphingidae-caterpillars, but the change is apparently always going on under the action of influences representing a general, fixed principle. So the brilliant optical colours occasioned by a morphological change of the scales also appear where the development of dark pigment is small, while these scales contain a great deal, if not solely, either red or yellow pigment; so making it rather difficult to admit that those pigmental colours can be going side by side with the structural colours, the latter making their appearance in order to fill up the place of the former. Nor can this theory solve the many biological questions, presenting themselves on account of the colour of butterflies, which my theory does in a full measure.

By comparison of series, first of individuals of the same species, then of those very little differentiated species which are probably only races of the same species, and further of species belonging to the same genus, it became quite clear to me that, with imagines of Pieridae at least, there is a continual change of colour going on in a definite direction, exactly concurring as a phenomenon with that observed in the caterpillars of the Sphingidae, and in no wise showing an accidental character or one connected with the surrounding. And further that this change consists in a course from red through orange and yellow into white or in reversed order, during which course often — but not always — black also appears more or less, but disappears again afterwards. And by a continued study of this course and of what reveals itself as being from an earlier or a later origin, I have got the conviction that it is in the first indicated order — the one in which red appears as the primary colour — that this evolution goes on in the above named family.

Once having asserted this, I have been able to interpret a great many phenomena which hitherto had not been explained in a satisfactory manner. And since this

could be effectuated with so many different phenomena, I think my views ought to seem so much the more likely to be right. Moreover all my pursuits in that line tend to lend force to my opinion on that subject — at least as to the main point — especially the studies I made during the summer of 1898 when I had the advantage of visiting the rich and newly classified collection of Pieridae in the British (South Kensington) Museum, and also the most superior collections of Msrss. Charles and René Oberthür at Rennes (France).

Not only has my conviction about the Pieridae always proved to be right, but also my supposition that the same thing occurs with the Papilionidae, the Lycaenidae and at least with a part of the Nymphalidae. Also on examining the rich series of Coleoptera belonging to Mr. René Oberthür, who had the kindness to lead me about in what was to me rather an unknown country, it became evident to me that even there the same thing happens. Merely on some minor points those afterstudies have somewhat altered my views.

I have not yet met with a rational contradiction of them in the different papers published at the same time or after mine on nearly related subjects, that is, those treating of the chemistry or chemical physiology of colours on the wings of butterflies, or of the results of experiments in reference to those colours by which the pupae of butterflies had been exposed to an abnormal temperature, or about investigations on the ontogenetic development of their wings in the pupae. In Dr. M. Baer's [1]) investigations for instance I did not find anything that could not be reconciled with my theory. On the contrary, his explanation of the green colour on the back of the hindwings of *Antocharis cardaminis* L. goes wonderfully well with what I said about it in my paper (page 250). Yet I was struck by a fact, which, though it has been noticed by

1) Ueber Bau und Farben der Flügelschuppen bei Tagfaltern (Zeitschrift für wissenschaftliche Zoologie, 65er Bd. 1er Heft, Leipzig, 1898).

Spuler before, seems to have escaped my attention then, that the pigment in the wings of butterflies is found in two different forms, mostly simply diffused through the chitin, but sometimes also in the form of granules. Remarkably enough this seemed to uphold my conjecture offered without my being acquainted with this fact, on pages 115 and 116 of my paper, that the changes of colour in butterflies might be brought about by a mere mining or sifting of pigment granules mostly in a chemical yet also sometimes in a mechanical way. So this seems to be possible after all. Dr. J. Urech's and other students' continued experiments in exposing pupae to a high or low temperature and the chemical-biological deductions therefrom, published by Dr. J. Urech [1]), although interesting, have not produced any thing decisive against my views. Unless indeed the fact that some rarely occurring colour-aberrations can be brought about by the immediate influence of abnormal conditions of temperature causing for instance an extraordinary formation of dark pigment or a chemical shifting of any other one. This I feel obliged to admit. But with reference to the ontogenetical and phylogenetical study of colour-evolution I cannot think it of much value. It will never do to conclude from such abnormal facts, never or only exceptionally occurring under natural conditions, with single individuals, that where in its normal development an increase of dark pigment occurs, this must be caused by an alteration of the temperature and its direct influence. The fact that the human skull can be artificially deformed and this even being a general custom with some wild tribes, cannot be of any valuable account in explaining the origin of dolichocephalism or of brachycephalism of human skulls [2]).

1) Ergebnisse von Temperatur-Experimenten an *Vanessa Io* L. (Illustrirte Zeitschrift für Entomologie, 1898).

Kenzeichnung und kritische Bemerkungen über Terminologisches, Wärmeenergetisches und Farbenevolution meiner erzielten Aberrationen von *Vanessa Io* und *urticae* (Zoologische Anzeiger, XXII Bd., n° 582, 13 März 1899).

2) It is just the same with all similar investigations, being high fashion now-a-days. I recommend reading on this subject Dr. Gräfin M. von Linden's Ver-

I have already demonstrated with many instances how a biological observation of several species of butterflies living either under very different or similar conditions is absolutely in opposition to such a theory. Two new instances have since come to my knowledge. The first was named by Dr. K. Jordan [1]), stating that the differences in the development of black on the upperside between the summer and spring broods of *Papilio Machaon* L. in Japan are the reverse of the differences in colour between the summer and spring broods of that butterfly in Europe. The other one relates to *Vanessa urticae* L. and seems doubly remarkable to me, as I have been particularly and amply digressing on this species, it having, moreover, played a notorious part in the above named experiments. In those experiments the var. *polaris* Stdgr. is always expressly named as a dark form from North-Europe (Lapland), its dark colour being considered as the consequence of its living in a colder climate. I had been obliged to state in my paper (on page 169) that the specimen of that var. *polaris* Stdgr. known to me do not much differ in colour from some dark Dutch ones, that happen to live here next to other lighter coloured ones, and now it appears to me that three English entomologists, at the meeting of the Entomological Society of London on Dec. 7th 1898 [2]), exhibited several specimens of that butterfly, partly caught, partly bred, all of them originally from Norway (69° 50′ N.), most resembling English

suche über den Einfluss äusserer Verhältnisse auf die Gestaltung der Schmetterlinge (Illustrierte Zeitschrift für Entomologie, IV). It is a well known fact that, by administering them alcohol, one can stay the growth of young dogs and so breed exceedingly tiny ones. But this does not explain why some races, as for instance Terriers or King Charles are so much smaller than Newfoundlanders or Ulmer-dogs! It is the great mistake Darwin made to derive from the abnormal phenomenon of an artificial selection the normal course of organic evolution and to base his theory of natural selection thereupon. That is the reason why it is getting more and more obvious that this theory is a false one.

1) An Examination of the Classification and some other results of Eimer's researches on Eastern Papilios: A Review and Reply (Novitates Zoologicae, vol. V, 1898).

2) Proceedings of the Entomological Society of London. 1898.

ones though the average was much darker than that of English examples, from which Norwegians only one or two approached var. *polaris* Stdgr. which was not actually represented. This seems to tend to the necessity of revoking that Northern race *polaris* Stdgr., and of admitting that also in the North of Europe the specimens of *Vanessa urticae* L. consist in darker and lighter-coloured ones, just as in the Netherlands, differing very little in colour from these latter ones, if doing at all so. If now Dr. Urech, though well-aware of the difficulty, still tries to explain the facts that the same difference in temperature with one species can have just the contrary effect with another, and that abnormal cold and abnormal heat sometimes can produce the same results in the same species, I shall not make so bold as to combat the scientific value of his reasoning, but I shall still have to doubt its applicableness to this subject. For this supposition in itself being rather hard to admit, with regard to the above-named difference in such nearly related species, as for instance the *Polyommatus Phlaeas* L. and *Ilerda Epicles* Godt. on which I wrote in my paper on pages 204 and 205, this explanation will not do where one sees exactly the same changes of colour manifesting themselves in races living in different countries, and even in individuals living next to one another in the same country, or in sexes of the same species, as is obvious to any one having the opportunity of indulging in a more ample contemplation of butterflies, not merely restricted to European species, from which even that most useful var. *polaris* Stdgr. now also must be excluded. As surely as these changes can not be explained by Dr. Urech's former theory, tending to the effect that where the molecular weight is increasing by better nourishment or a warmer climate the colour also darkens, they can neither be accounted for in this manner. They indicate a phenomenon of evolution evidently going on orthogenetically through the whole world without heeding any difference of temperature. Colour-evolution of Sphingidae-caterpillars is unquestionably also absolutely independent of

the direct influence of temperature. That, however, such differences might not, without a direct influence, under special conditions act as a stimulus to change of colour, I also feel bound to contest. Every where, even out of the boundaries of animal life, evolutions show the phenomenon of genepistasy and the excitement there from by internal or external influences acting as a stimulus. How strongly this phenomenon — which in a former study on the process of atrophy of the horn of Sphingidae-caterpillars I indicated clearly — shows itself in the course of colour-evolution in butterflies and their caterpillars, is to me quite an undoubted fact. That stimulating influences must act thereupon seems a necessary consequence; and why should those influences of temperature not be able to have that effect?

Of very little meaning — though I have to mention it here also by the way — is, with regard to the topics of my studies, Mr. Roland Trimen's recent speech on seasonal dimorphism in Lepidoptera [1]) as it contains simply a report of work done by others, but no new views. I think, however, he might have mentioned something of what I communicated concerning his special subject, if only (for completeness' sake) my observations concerning *Cyllo Leda* L. made in Java, the more so, as I presented a copy of my paper to the Entomological Society of London. It struck me also that Dr. Dixey still considers *Catopsilia Crocale* Cram. and *C. Pomona* F. including *C. Catilla* Cram. as seasonal forms of one species which Mr. de Nicéville thinks doubtful, all the supposed distinctive characters proving quite inconstant and breaking down when large numbers of specimens are compared. Even as far back as 1890 I published — though in French [2]) — such ample statements about this peregrinating butterfly that its identity cannot leave any doubt

1) Proceedings of the Entomological Society of London, 1898.

2) Observations sur des vols de Lépidoptères aux Indes-Orientales Neerlandaises et considérations sur la nature probable de ce phénomène (Natuurkundig Tijdschrift voor Ned.-Indië, Dl. L).

whatever, nor can there be left the least idea of seasonal forms. But then, what can be the cause of all those changes of colour? Well, the theory of temperature does not answer this question; but my theory does.

And the many colour-variations in American *Callydrias*-species and in the Australian *Catopsilia Gorgophone* Bsd., stated by Dr. Dixey, will surely have to be explained in the same way.

A great deal more important is Dr. Gräfin M. von Linden's work »Untersuchungen über die Entwicklung der Zeichnung des Schmetterlingsflügels in der Puppe" [1]). As is said on page 117 of my paper I have always thought these ontogenetical investigations the weak point of my theory, because they disclosed facts, apparently not to be reconciled with it, and yet in spite of all possible considerations being of no small significance. Indeed those considerations are rather important. Not only do we not find here such well separated consecutive ontogenetical stadia as are so clearly visible in caterpillars, but we also cannot dispose of such a relatively long lapse of time, at hand for the observation of embryological changes in many other animals, thus greatly facilitating it. And time is a valuable thing in this matter, as the phylogenesis, that has to be traced, has not taken place constantly and regularly, but now quicker then slower, with periods of genepistasy of extremely unequal duration, and not at all following the same course either on both the wing-surfaces or their parts. Then the well-known phenomenon of some phyletical stadia happening to fall away in the ontogenesis is to be added. Now in the changes which the wings of the not yet full grown butterfly in the pupa undergo during the 48 hours before coming out of the butterfly, all this has to be traced as it has developed in the course of perhaps many ten thousands of years. And still more this does not

1) Zeitschrift für wissenschaftliche Zoologie, 65er Bd. 1er Heft, Leipzig, 1898.

regard forms but colours, while several facts mentioned by myself and others met with by Dr. v. Bemmelen and Dr. Gräfin von Linden, indicate that colours showing themselves within the skin of the pupa, are sometimes altered by their coming into contact with light or air, and so probably those same colours may at an earlier period also have been different in the full-grown animal from what ontogenetically is found to-day. Also the possibility of other influences acting on the insect of to-day, even though not yet full-grown, cannot be denied, influences different from those to which its ancestors were exposed during the phylogenesis, that may cause such differences. Considering all this, it surely would be presumptuous to attach too much importance as decisive in itself to the results of such investigations, but still they remain facts of great significance which one have to be reckoned with.

Dr. Gräfin von Linden has now been investigating in that manner 5 butterflies viz. *Papilio Machaon* L., *Papilio Podalirius* L., *Thais Polyxena* Schiff., *Vanessa urticae* L. and *Vanessa Levana* L., and she has done it pretty carefully. Unfortunately, however, there lies, if I may say so here, spread over these investigations a veil that will have to be removed before they are fit for use. Quite infatuated by the assertions of the late Prof. Dr. Eimer, in whose last work she has, as I believe, taken a large part as his assistant, she adopts all his views in their full consequences, among which views there are two that I most decidedly must reject, though being of the same opinion as Dr. Eimer on many points. Now these two views happen to be of the greatest importance concerning the subject treated by me. They are firstly Dr. Eimer's well-known bands-and-spots-theory and secondly one in which the form of the colour spots on the wings of butterflies is considered as a thing by itself and independent of the colour. Leaving alone now the value of his theory as to the higher animals — though that has been also lately contradicted by H. Meerwarth with regard to the changes in the colour-pattern of bird-

feathers [1]). — I have in my paper demonstrated largely for what reasons I can in no wise accept it with regard to the Lepidoptera. I do not wish to reiterate those reasons, that are fully decisive for me, on this occasion. I only want to point out how Dr. K. Jordan in his above named paper, has exposed Dr. Eimer's assertions in such a vigorous manner, that I fear they will not readily recover from the blow.

Concerning the independence of the forms of the colour-pattern, in which matter Dr. Eimer's opinion is directly opposite to that of Prof. Dr. A. Weismann, I declared in my paper (on page 90 and further on) that I sympathise with the opinion of the latter. Dr. Gräfin von Linden, from the fact observed by her that in the ontogenetical development of the wings of *Papilio Machaon* L., the scales in some parts of the wings are coloured earlier than in others, tends to the conclusion of a difference between primary colour and colour-pattern; but in reality nothing is revealed here but the most common phenomenon of the great diversity in which colour-evolution is proceeding, a thing whereby likewise an appearance sooner or later of the pattern on the fore- or the hindwings may be occasioned, which she also endeavours to connect with the laws of Dr. Eimer. On the other hand my view was considerably strengthened by a special declaration about what had formerly been observed by Dr. Urech concerning this point in the ontogenesis of *Pieris brassicae* L., absolutely confirming Weismann's verdict on that matter, with some small supplementary additions [2]).

Now Dr. Gräfin von Linden seems so very anxious to adapt her observations to Dr. Eimer's views, and her endeavouring to do so exercises such a predominating influence on her work, that whosoever intends to make use of the published results has constantly to bear that in mind

1) Zool. Jahrb. Abth. f. Syst. Bd. XI. However only known to me from a report in the Naturwissenschaftliche Wochenschrift, 16 October 1898.

2) Einige Bemerkungen zum zeitlichen Auftreten der Schuppen-Pigmentstoffe von *Pieris brassicae* (Illustrirte Zeitschrift für Entomologie, 1899).

and to separate the one from the other in order to come to the right conclusion.

So for instance, this experimentist concludes by saying that, as a result of her investigations, the ontogenetical order of colours on the wings is the same as has been observed by Urech and also indicated by Eimer as the phylogenesis of Lepidoptera, namely this: Yellow appears first and is followed by orange, lighter and darker red, red-brown and finally by black, on which sometimes blue is seen as an optical colour; a verdict not at all agreeing with my supposition that red appears as primary colour, slowly turning, through orange and yellow, into white; and that often, but not always, during this process, — that is: sometimes still on the red colour, but as well on the orange or yellow [1]), black will appear, spreading out more or less, to be finally also driven away by white; which means, indeed, a fading-process from red into white, during which sometimes black appears for a while and in a secondary way.

Now let us see what those experiments have in reality produced.

The earliest place in which she finds pigment in all the butterflies examined by her, is the wing itself, only later on it appears in the wing-scales. And there she always found in all the five species red just as well as yellow pigment, the most red pigment in the species that still presents the most of it in its full-grown state, *Thais Polyxena* Schiff., pretty much in both *Vanessae*, least in both *Papilios*, being also in a full-grown state the lightest coloured of these butterflies, thus — as Miss Newbegin does not fail to observe — the red pigment being always present in the oldest form. Next to yellow indeed, but that this red must necessarily have grown out of that yellow

1) Perhaps also on white, even when this has become the general colour. If so, black in some species (as *Pieris brassicae* L.) might be not, as I used to think, a remains of an earlier black, but, indeed, a newly appearing colour which would explain the results of the ontogenetical investigation.

and is accordingly to be considered as the younger colour, does not seem to be quite a matter of course.

The simple fact observed by Dr. Gräfin von Linden that in the ontogenesis of *P. Machaon* L. the early orange-yellow spot on the hind wings will turn to red afterwards, is certainly not sufficient, where all similar observations still remain so incertain to lead to such general deductions, the more so as that spot later on turning to a dark red-brown, betrays the interference of another dark pigment. On the contrary it is quite sure that though these experiments, testifying to a constant preoccupation with Dr. Eimer's colour-pattern, are not all one might wish them to be regarding the observation of colour-evolution, they still give the impression of the ontogenetical colour, specially of *P. Podalirius* L. presenting a remarkably stronger tint of yellow than the actual colour of that butterfly shows now-a-days, which seems conformable to a tendency to fading in colour.

Neither can it be denied that where a little red pigment is found in the oldest form next to a great deal more of yellow pigment, the further ontogenetical course does in no wise show a notable increase of the red colour, as indeed it ought to if the yellow were slowly turning into red. But there is more. As has clearly been demonstrated by many experiments, also by those of Dr. v. Bemmelen, the oldest ontogenetical state does not go further back than to the relatively not very remote period in which many of the now living, nearly related, species of the same genus were differentiated from one another. Now my supposition is that red was the general colour before the *Pieridae*, *Papilionidae*, *Lycaenidae* and *Nymphalidae* were differentiated, that is in such a remote period that those investigations cannot possibly recover anything thereof. If then in the oldest investigable period some red pigment is still always found, but ever lessening in the same measure as the now living butterflies have become paler and more distant from that original colour, this seems to me to be wunderfully well in accord with my theory, indeed strongly

supports it. In the remotest investigable period the red colour in both *Papilios* surely must haved turned nearly all to yellow, hence the yellow one is found there so abundantly and the red one has become so scarce. The groups to which these *Papilios* belong, especially those of *Podalirius*, in some species of which the scales are wholly disappearing, do contain, according to my theory, butterflies in a far advanced state of colour-evolution. I think it quite a matter of course that, where black appears upon red, the colour is at first darkened thereby, and I never intended to deny that. But a single look at the family of the *Pieridae* is enough to point out that black does just as often appear upon orange and yellow without any intervention of red, and that is not at all explained by the above named series of succeeding colours. In my theory, however, it can be explained without the least difficulty. Finally I have to point to the fact that Dr. Gräfin von Linden (though it is not spoken of in the account) in the report of her investigations about *Vanessa levana* L., *prorsa* L. particularly mentions that in this species white does come on by driving away black, that is: as the final colour. Exactly coinciding with my views, though it is possible that this white colour may be an optical colour; for optically white scales are bare of pigment and accordingly lost all pigment when black was driven out, which indeed with regard to the final colour agrees perfectly well with my views, as can be seen on page 238 and so on of my paper.

So if I may take the liberty to judge Dr. Gräfin von Linden's interesting study after the revealed facts more than after the written words, I find a really most valuable confirmation of what my investigations have led me to accept as likely to be true [1]).

1) I only came to know of Dr. Gräfin M. von Linden's critical study of my paper on evolution of colour of Pieridae published in the „Illustrierte Zeitschrift für Entomologie, IV, p. 19 (1 Oct. 1899)" after having done writing all this. I do not think it of any use to refer to her paper after all the above said. Unfortunately this learned authoress also appears not to be a genuine Lepidopterologist

I still have to mention here a paper by J. A. D. in Nature (Nr. 1544) headed »Evolution without Selection", directed against me. As this article does not contain anything but a personal attack without a single scientific argument, I cannot respond to it in this periodical. I tried to do so in »Nature", but the Editors, who had several columns to spare for this attack, were not so courteous as to open those columns to my answer too.

The conclusion of all these investigations seems to me to be a great deal more to the advantage of my hypothesis than to the contrary, howsoever strange they may appear to some people. And in fact I do not consider myself as beaten. But, those that intend to attack my theory seriously, will certainly have to combat in the first place the phenomenon denominated »Evolution of Colour", that I believe to have established in the *Sphingidae*-caterpillars. If my observations on this point are wrong, let it be demonstrated. Does anybody know how to interpret them otherwise? Perhaps in the way indicated in former years by Prof. E. B. Poulton? [1]). Miss Newbegin from her partial chemical standpoint does indeed think that explanation quite correct, but since I have pointed out that the change of colour of these cater-

and cannot therefore examine and compare the facts upon which my opinions are based. And I think she has not quite understood my standpoint as to Eimer's theory of „das Organische Wachsen". So at the end of her study she says that I pretend to reject the basis of that theory and yet continually point out facts clearly confirming it. This doubtless alludes to page 275 of my paper, where I say that I believe his theory ought to be absolutely rejected. However what is said there has nothing whatever to do with Eimer's theory of „das Organische Wachsen", but refers to his bands- and pattern theory. With the first one I do agree pretty well on the whole.

I met with more similar inadvertencies and of course they are narrowly connected with the authoress' judgment of my study. But when she says that my thesis of a hereditary stress ruling the colour-evolution does not explain the cause of that phenomenon, she most certainly is quite right. About the ultimate cause I have said little. Does this however attack the justness of my observations as to this phenomenon and the importance of its existence?

1) E. B. Poulton. The Essential Nature of the Colouring of Phytophagous Larvae (and their Pupae); with an Account of some Experiments upon the

pillars is a rule, evidently proceeding ontogenetically under a hereditary stress, manifesting itself in all species of that family wheresoever in the world they may live, and though having indeed a very different course still bound in its appearance to definite periods of the general development of the animal, I do think this theory rather hard to be still admitted. At all events the non-existence of colour-evolution in these caterpillars will first have to be proved, for where this cannot be denied, the action of this same phenomenon with regard to the expansion of colour in imagines has positively to be considered as a very likely one.

Chemical, microscopical and ontogenetical investigations may be continued as to its course, though rather in a more systematical way than has been done up to now, if it might be of any use. First of all one should try to know of all the appearing colours in any definite butterfly, whether they are pigmental or structural colours. Especially this is needed in regard to those butterflies whose colour-evolution is investigated ontogenetically. For as only pigmental colours are of importance for the study of colour-evolution it must indubitably lead to confusion, if they are not properly distinguished. Now though Miss Newbegin is of opinion that optical colours cannot, of course, be found at an ontogenetical investigation yet Dr. Gräfin von Linden has positively found them. Even the white colour in the wing-tip of *Danais Plexippus* L. is according to the investigation of A. G. Goldsborough Mayer structural and presumably it will be quite the same with the white *Vanessa*-spots of Dr. v. Bemmelen. All such investigations should further specially direct attention to the colours and their development in such butterflies where the prime colour differs in the same species, in sexes, races or forms, and so one colour

Relations between the Colour of such Larvae and that of their Food-plants. Proc. Royal Society London, Vol. XXXVIII, 1885; and E. B. Poulton: The Experimental Proof that the Colours of certain Lepidopterous Larvae are largely due to modified Plantpigments derived from Food. Proc. Royal Society London, IV, 1893.

is always replacing another. For the ontogenetical investigation, however, mostly tropical species are wanted; merely the difference between both sexes of *Antocharis cardaminis* L. can also be studied in Europe. The ♂ of this butterfly can perhaps lead to a very important investigation. It may be admitted as it seems from the investigation of *Pieris brassicae* L. by Dr. Urech and Dr. v. Bemmelen that in the oldest investigable state of this butterfly there is absolutely no red pigment to be found, but only yellow (green). Now this species, to my theory is very much advanced in colour-evolution, even much farther than *Papilio Podalirius* L. in which indeed, some red (though very little) has yet been found. *A. cardaminis* L. also is very advanced, however not so far as the above named *Pieris*, as the ♂ shows still a little orange-tinted red on the wings. If this view be right some red also must still be existing in the oldest investigable state of *A. cardaminis* L., that is in the wing, before the pigment has penetrated into the scales; though probably very little, and also faded into orange. Now as the remaining quantity of red can only be so very small, may be it is impossible to trace it in this case, but yet it seems desirable that one should try to do so, for if it were found, however little it might be, it would give strong evidence to the justness of my view. Such an investigation, however, ought to be done most accurately and closely directed to the point. Of course I allude to the pupae of ♂♂, with the ♀♀ the chance of finding still some red or orange is certainly very small. If indeed those colours could still be found in the ♀ pupae, the question might be considered as very near to its solution. But from the tropical countries where such remarkable polymorphical forms are found, as well as such very large Lepidoptera, true knowledge in this matter will have to come forth. Only there, too, the forms of *Papilionidae* and *Pieridae* whose wings have already more or less lost their scales, can be investigated. In Europe only the ontogenetical study of the almost scale-bare spots in ♀♀ *Aporia crataegi* L. still can be of

some use. I do not attach any value to investigations of temperature or of cross-breeding in this matter.

Meanwhile there has been announced as prize-question by Czar Nicholas II for the International Congress of Zoology in 1901 to be held in Germany, an investigation as to the influence of light on the development of the colours in Lepidoptera, and into the causes of such deviations in colour, form and structure, appearing in those parts of these insects that are covered in their state of rest. Now such an investigation, shall it be of any value, will have to reckon with my theory of colour-evolution. In fact according to that, the difference in colour is — at least in the imagines and caterpillars of Lepidoptera — principally the consequence of a hereditary evolution, which though perhaps not wholly excluding the influence of light, does indeed reduce it to a thing of little significance; and so if that influence shall be proved, my theory must also be proved to be erroneous, these two being inconsistent with each other. Only in a very secondary way some of that influence still remains possible, as for instance was stated by Prof. Poulton and Meldola regarding some *Sphingidae*-caterpillars, though these too are subject to colour-evolution. I do not think it quite impossible that light can indeed act a part among the still unknown local influences — I call them geographical ones — that will alter the colour of imagines now and then, as well as that some abnormal chemical changes can be occasioned in the wings of butterflies by letting rays of light of any definite colour act on the pupae. When judging the answers to this prize-question it will be wise not to overlook the warning words on pages 80—85 of my paper on *Sphingidae*-caterpillars and also what I wrote about the (in their state of rest) partly covered wings of Lepidoptera, on pages 245—249 of my study on the *Pieridae*.

It must not be forgotten that of a great many Lepidoptera, resting with their wings folded up, the whole

upperside is for the greater part of their life, deprived of the action of light, as indeed of all those real sun-butterflies, that fly almost exclusively in the sunshine and even then only for some hours, neither that the upperside of the hindwings of many Heterocera, as *Catocala* and *Ophideres*, as well as of several *Sphingidae*, that is always covered by the forewings in the day-time, is nevertheless remarkably coloured. With regard to the pupae the influence of the light is of far greater significance, as has been proved by many investigations. Yet it seems not to be so much the action of light on the pupa itself as indeed on the caterpillar a little while before it changes into a pupa. But in this matter also one had better be very cautious and not judge by a few single results, as Mr. Bordage in his communications at the Cambridge Congress [1]) clearly pointed out, and in the first place some pupae formed in similar normal conditions ought to be closely observed. I beg to refer once more to my study on *Pieridae* (pages 174—175) and to what I said there concerning varieties of *Eugonia autumnaria* Wemb. bred by Merrifield. Of *Papilio Memnon* L. for instance there exist bark-coloured ones mixed with some white and green, and also wholly green pupae, the former perfectly rendering the colour of the bark of a tree speckled here and there with some green moss, and so resembling also the branches of the tree on which the caterpillar lives, the other one resembling the citrus-leaves on which it feeds. Yet I have often bred both forms under absolutely similar conditions of light and environment. Just so with pupae of other species. On Java I also happened to know the three forms of pupae of *Danais Chrysippus* L., pale rose-coloured, lively green and waxlike white ones, mentioned by Bordage, but I also observed that part of those green pupae,

1) E. Bordage. Expériences sur la relation qui existe entre la couleur du milieu et la couleur des chrysalides de certains lépidoptères (Proceedings of the fourth International Congress of Zoology. London, 1899).

though remaining under the same conditions as the others that did not change, began to change colour later on becoming a waxlike white without my being able to trace the cause thereof. Exactly in the same manner I saw from a certain number of green pupae of *Danais Genutia* Cram. after a while some becoming pale rose-coloured and the rest remaining green. More similar facts have always kept me from saying much as yet about the results obtained in the matter by other authors especially by Poulton, though many a time I have made observations perfectly agreeing with theirs. I thought it prudent to remain on the reserve. Neither do I think it impossible that a hereditary colour-evolution should exist in the pupae, though it could not be traced as yet. In that case the above named action probably ought to be considered principally as a mere stimulus, and so the colour-polymorphism must be here also the expression of stadia in a proceeding course of colour-evolution. It attracted my special attention to hear from Mr. Bordage that he had obtained pupae not like normal ones, uniformly polished, looking like gold or silver, but with dark brown stripes and spots on the metallic hue, by breeding caterpillars of *Euploea Goudoti* Bsd. in complete darkness. While indeed the pupa of *Euploea Midamus* L. in Java always uniformly has that same golden or silvery hue, the pupa of *Euploea leucostictos* Gmel. in that country always has such brown spots or stripes on the metallic hue, so that the abnormal condition gives birth in *Euploea Goudoti* Bsd. to what in the nearly related *Euploea leucostictos* Gmel. still or already appears as normal. With all this, as already said, one will have to reckon seriously when judging of the eventual answers to the prize-question.

The Hague, September 1899.